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313

THE GASES IN LIVING PLANTS.¹

BY J. C. ARTHUR.²

The present state of knowledge regarding the kinds, sources and movement of gases in plants does not constitute a completed volume. There is much yet to be learned, old views are to be corrected, and alleged facts are to be more firmly established. The subject is thoroughly modern, the first writer to give any connected and intelligent account of the behavior of gases in connection with living plants being De Saussure in his brilliant and epoch-making work describing his chemical researches upon vegetation, published in 1804.

THE COURSE OF DISCOVERY UP TO 1865.

The various life functions of plants have been slowly established by first assuming them to be individually the same as those of animals, and from this basis gradually evolving their true nature. The early naturalists saw nothing in plants that suggested lungs or the movement of air, and it was not till the time of Malpighi, 1671, that breathing was supposed to have any part in the plant economy. He saw in the wood vessels, known then and long afterward as spiral vessels, an analogous

¹ Read before the Biological Section of the Amer. Assoc. Adv. Science, in Washington, August, 1891.

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set of organs to the tracheæ of insects, and therefore believed them to have the same office. His views were accepted by the Englishmen, Grew and Ray, who wrote about the same time, but found no supporters in Germany or France. The views of Malpighi, who in many respects was far in advance of the other botanists of his age, fell into obscurity, insomuch that even the existence of ducts was finally denied.

The subject was not revived until 1715, when Nieuwentyt demonstrated the presence of air in plants by placing sections of stems in water under an air pump. The demonstration was better performed by Christian Wolff, who was a philosophical naturalist of much insight. He placed leaves, wood, and other parts of plants, in water, freed from air, under the air pump, and after seeing the bubbles rise from the tissues as the air was exhausted from the receiver, he allowed the air to re-enter the receiver, and found that the tissues were at once filled with water, and that some kinds were thereby made so heavy as to sink.

In England, a few years afterward (1727), Stephen Hales, the real founder of experimental vegetable physiology, repeated and improved upon the air pump experiments, but used his knowledge to explain the life processes in a different manner from his predecessors. He combined the fact that gases are recovered from plants by dry distillation and fermentation to support a well arranged theory of the use of gases in forming the solid parts of plants. The use of gases by plants was, therefore, according to Hales, a part of the subject of the nutrition of plants.

But this small advance led to no further developments, and was again lost sight of for many years. After nearly half a century, in 1771, Priestley hit upon a discovery which, coming as it did only three years before the discovery of oxygen, and only shortly before the re-organization of chemical theories by Lavoisier and others, proved very fruitful.

Priestley's discovery was simple enough, amounting only to the fact that plants give off oxygen. He tells of his discovery in an interesting way, and I, therefore, quote a few paragraphs

from his communication to the Royal Society, announcing the matter:

“The quantity of air which even a small flame requires to keep it burning is prodigious. It is generally said that an ordinary candle consumes, as it is called, about a gallon in a minute. Considering this amazing consumption of air, by fires of all kinds, volcanoes, etc., it becomes a great object of philosophical inquiry, to ascertain what change is made in the constitution of the air by flame, and to discover what provision there is in Nature for remedying the injury which the atmosphere receives by this means.

“I flatter myself that I have accidentally hit upon a method of restoring air which has been injured by the burning of candles, and that I have discovered at least one of the restoratives which Nature employs for this purpose. It is vegetation. * * * One might have imagined that, since common air is necessary to vegetable as well as to animal life, both plants and animals had affected it in the same manner, and I own I had that expectation when I first put a sprig of mint in a glass jar standing inverted in a vessel of water; but when it had continued growing there for some months, I found that the air would neither extinguish a candle nor was it at all inconvenient to a mouse which I put into it. * * * Finding that candles burn very well in air in which plants had grown a long time, and having had some reason to think that there was something attending vegetation which restored air that had been injured by respiration, I thought it was possible that the same process might also restore the air that had been injured by the burning of candles. Accordingly, on August 17, 1771, I put a sprig of mint into a quantity of air, in which a wax candle had burned out, and found that on August 27 another candle burned perfectly well in it. This experiment I repeated, without the least variation in the event, not less than eight or ten times in the remainder of the summer.”

Had Priestley had the good fortune to have set his jar containing green sprigs into direct sunlight, he would have made an additional discovery of almost equal importance. But the world did not wait long till Ingenhousz went over the ground

and discovered (1779) that light was an essential factor in restoring air, and that by the aid of sunlight he could perform in a few hours the experiments which took Priestley five or six days.

In 1800 Senebier added the discovery that plants obtain all their carbon from carbon dioxide, but fell into the error of supposing that part, at least, of this gas was taken up by the plant through its roots, an error that has proved extremely tenacious, existing in our text books to the present day, although repeatedly and fully disproven.

We have now arrived at the time of De Saussure (1804), who, with his superior chemical knowledge, placed the whole subject in excellent shape. He distinguished between carbon assimilation and true respiration. He dealt with the subject quantitatively, and showed that there was a definite relation between the carbon dioxide taken up by the plant and the oxygen evolved by the action of light. He clearly pointed out that the presence of oxygen was as essential to the growth of plants as to animals, the most active parts, such as green leaves, opening flowers, etc., requiring the most, and that this requirement had no relation to the presence of light.

De Saussure also pointed out that while plants receive their supply of carbon dioxide for assimilation, and oxygen for respiration directly from the atmosphere, yet the nitrogen, which is an essential constituent of their organization and by far the most abundant gas in the atmosphere is not utilized by plants in the gaseous form.

Having now established that plants contain gases, that these gases are the same as those of the atmosphere surrounding the plant, that oxygen and carbon dioxide are made use of in their gaseous forms in the life processes of plants, while nitrogen as a gas is not actively connected with the life of plants, and having established these facts with a wealth of accurate experiment and logical deduction that permitted no doubt of the truth, it was left to De Saussure's successors to elaborate the structure which he had so ably built, without being called upon to again readjust the foundations.

It was over thirty years before a work of importance in this line again appeared. In 1837 Dutrochet published his anatomical and physiological memoirs, in which he carefully studied the structure of vegetable organs as well as their functions. He was the first to rightly point out the relations of the cavities in plants to the movement of gases in respiration, that only cells with chlorophyll are able to decompose carbon dioxide, and to distinguish sharply between respiration and assimilation. But although he recognized the essentially different character of the two processes, respiration and assimilation, yet he used the erroneous and absurd nomenclature of the time, and called them nocturnal and diurnal respiration. The weight of his example did much to fix the terms in popular usage, where they still persist, in spite of the protests of every able investigator and writer upon the subject since; and even though the matter was set right by Garreau in 1851, who did admirable work upon plant respiration.

In 1865 appeared the handbook of experimental physiology of plants by Julius Sachs, the founder of the modern school of vegetable physiologists. The work was comprehensive, well balanced, and replete with clear ideas of the theoretical bearing and logical association of the facts.

The author's laboratory at Würzburg, where he shortly became established, has been the school from which most of the great plant physiologists of the present have received instruction and from which all have drawn inspiration. It is sad that its doors should now be darkened by the mists that have gathered over the intellect of its honored director.

In the handbook of Sachs a chapter is devoted to each of the three branches of the subject; aeration, or the movement of gases in the plant; respiration, or the action of atmospheric oxygen; and the effect of light upon vegetation, chiefly in assimilation. Each of the topics is treated in a clear and masterly manner.

NATIONALITY OF DISCOVERERS AND WRITERS.

Having traced the growth of knowledge regarding the vital relations of gases to plants up to the time when it was possible

to present the subject in a reasonably complete and well balanced manner, it will be more satisfactory to drop the chronological method of treatment, and to outline the salient features of the subject as they are understood at the present time. Before doing so, however, it will not be unprofitable to glance for a few moments at the parts which the several nations have played in this growth of knowledge, and at the reciprocal influence which has been exerted upon the teachers of those countries.

Science in its highest aspects has always been, as at the present time, the property of the whole world, knowing no political restraint or nationality. The barrier of language, however, has had much to do with retarding the diffusion of knowledge from the original sources of discovery into the text books, which serve as the means of enlightenment for the mass of learners.

The great discoverers and thinkers in our present subject, since the days of Malpighi, an Italian, have been either French, German or English. The Germans, before 1865, made no discoveries of commanding importance, and even their text books barely gave a true account of the subject as known at the time. Link, in 1807, ignored the all-important discoveries of Senebier and De Saussure, the more readily, doubtless, because they were Frenchmen. Twenty-five years afterward De Candolle's general treatise was translated from the French and became one of the most influential text books in Germany.

The chief activity among Englishmen occurred before 1800, and brought forward the names of Hales, Priestley and Ingenhousz. The advanced work was taken up by Frenchmen after 1800, among whom Senebier, De Saussure, Dutrochet and Boussingault are the most conspicuous investigators.

It is chiefly the French botanists, particularly De Candolle and Dutrochet, who have had the most potent and lasting influence upon the popular conceptions of the English regarding vegetable physiology. To them we can also trace a number of errors and omissions which figure in our school text books at the present time. De Candolle was the author of the

imaginary "spongioles" upon the root tips, which still have a sort of backwoods existence in the minds of some persons, although practically eradicated from the text books. He subscribed to the dual respiration of plants by which they gave off oxygen in daylight and carbon dioxide in darkness, which is still taught by certain American text books. In other American text books, which are still standard, a reaction is shown by the suppression of any suitable account of respiration proper, this important subject being referred to only incidentally in a line or two in connection with a short account of the use plants make of stored food material. Thus, in the latest revised edition of Gray's *Lessons in Botany*, as in the preceding edition, barely three lines are devoted to respiration, while two pages are given to assimilation. This work also teaches the incorrect doctrine³ that carbon dioxide beside reaching the plant through the surface of the leaves, "is absorbed by the roots of plants, either as dissolved in the water they imbibe, or in the form of gas in the interstices of the soil." In Bessey's *Botany*, first issued in 1880, respiration is treated in essentially the same brief manner, and it is curious to note that the unusually complete index to the work does not contain the words gas, breathing, or respiration.

The modern phase of plant physiology may be said to have been introduced to English speaking students by the translation of Sach's text book in 1875, and reinforced by the appearance of Goodale's work in 1885, on this side of the Atlantic, and of Vines' work the following year in England. In these works the balance between respiration, assimilation and the physical movement of gases is fairly well maintained. Another work in English, less pretentious, but equally accurate and discriminating with the last mentioned, and antedating them, should be spoken of here, that of Johnson's *How Crops Feed*, published in 1870. The work was deservedly popular, and is still a source of exact information.

³In the discussion which followed the reading of this paper, Prof. Geo. L. Goodale gave Dr. Gray's reasons for retaining his early views. It was Dr. Gray's belief that his statement would prove, upon more extended investigations, to be essentially correct. Prof. W. H. Brewer spoke in further support of the conservative views of Dr. Gray.